

Technical University of Denmark



Evolution of boldness and life-history in response to selective harvesting

Andersen, Ken Haste; Marty, Lise; Arlinghaus, Robert

Published in:
Canadian Journal of Fisheries and Aquatic Sciences

Link to article, DOI:
[10.1139/cjfas-2016-0350](https://doi.org/10.1139/cjfas-2016-0350)

Publication date:
2017

Document Version
Peer reviewed version

[Link back to DTU Orbit](#)

Citation (APA):
Andersen, K. H., Marty, L., & Arlinghaus, R. (2017). Evolution of boldness and life-history in response to selective harvesting. Canadian Journal of Fisheries and Aquatic Sciences. DOI: 10.1139/cjfas-2016-0350

DTU Library

Technical Information Center of Denmark

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Evolution of boldness and life-history in response to selective

2 **harvesting**

4 Ken H. Andersen¹, Lise Marty^{1,2}, and Robert Arlinghaus^{3,4}

6 1 Centre for Ocean Life, DTU Aqua, Jægersborg Allé 1, 2920 Charlottenlund, Denmark

2 Institut Pierre Louis d'Epidémiologie et de Santé Publique, UMR_S 1136 INSERM et

8 UPMC, 56 Bd. Vincent Auriol, CS 81393, 75646 Paris cedex 13, France

3 Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology

10 and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany

4 Division of Integrative Fisheries Management, Albrecht-Daniel Thaer Institute of

12 Agricultural and Horticultural Sciences, Faculty of Life Sciences, Philippstrasse 13, Haus

7, 10115 Berlin, Germany

14

Corresponding author: Ken H. Andersen (email: kha@aqua.dtu.dk)

16

18

20 *Abstract*

Whether intensive harvesting alters the behavioural repertoire of exploited fishes is
22 currently unknown, but plausible. We extend a fish life-history model to account for
boldness as a personality trait that affects foraging intensity, which affects energy
24 intake and risk from predation and fishing gear. We systematically investigate life-
history and behavioral trait evolution along the boldness-timidity axis in response to
26 the full range of common selectivity and exploitation patterns in fisheries. In agreement
with previous studies we find that any type of harvesting selects for fast life histories
28 and that merely elevated, yet unselective, fishing mortality favors boldness. We also
find that timid-selective fishing (which can be expected in selected species targeted by
30 active gear types) selects for increased boldness. By contrast, increased timidity is
predicted when fishing targets bolder individuals common to passive gears, whether in
32 combination with selection on size or not. Altered behavior caused by intensive
harvesting should be commonplace in nature, which can have far-reaching ecological,
34 evolutionary and managerial impacts. Evolution of timidity is expected to strongly
erode catchability, which will negatively affect human well-being and influence the
36 reliability of stock assessments that rely on fishery-dependent data.

38 **Key words:** fisheries-induced evolution, timidity syndrome, personality traits, selection
gradients, life-history evolution

40

42 **Résumé**

44 Il est actuellement encore incertain, mais plausible, que la pêche intensive puisse
46 altérer le répertoire de comportements des poissons exploités. Nous étendons un
48 modèle décrivant l'histoire de vie des poissons pour y incorporer un trait de
50 personnalité, l'audace, et examiner de façon systématique l'évolution des traits
52 d'histoire de vie et comportementaux le long de l'axe audace-timidité, en réponse à
54 différents types de sélectivité et d'exploitation couramment rencontrés dans les
56 pêcheries. En accord avec les études précédents, nous montrons que tous les types
58 d'exploitation favorisent une histoire de vie plus rapide et qu'une faible augmentation
de mortalité, même non sélective, favorisent une plus grande audace. A l'inverse, une
timidité accrue est prédite quand la pêche cible les individus les plus audacieux, cas
typique des engins de pêche passifs, que ce soit en combinaison avec la taille ou non.
Les modifications du comportement causés par la pêche intensive sont probablement
courants dans la nature, ce qui peut avoir d'importantes conséquences écologiques,
évolutives et en termes de gestion. En particulier, l'évolution vers une plus grande
timidité peut éroder l'attrapabilité, affectant le bien-être des pêcheurs et la fiabilité des
évaluations de stock reposant sur des données dépendantes de la pêche.

60 Introduction

Assuming that phenotypes expressed by animals in the wild have a heritable basis
62 (Mousseau & Roff 1987; Dochtermann et al. 2015), harvesting can cause phenotypic
and genetic, i.e., evolutionary, changes in exploited populations (Jørgensen et al. 2007;
64 Allendorf & Hard 2009). For harvesting-induced evolution of life-history traits, such as
maturation size or reproductive investment, to occur, it is sufficient that the mortality
66 induced by humans is elevated beyond natural mortality levels because the now altered
fitness landscape will select for different phenotypes than natural selection alone
68 would favor (Dieckmann & Heino 2007; Heino et al. 2015). Evolutionary responses
caused by fisheries will be magnified if fishing mortality is not only elevated but
70 selective for fitness-related traits, such as body size (e.g., Edeline et al. 2007;
Matsumura et al. 2011; Heino et al. 2015).

72
Most fishing gear is size-selective, preferentially capturing a certain range of sizes (e.g.,
74 in gill nets) or predominantly harvesting individuals that are larger than a minimum
retainment size (e.g., in trawls). A key finding of a range of models and experiments
76 studying the consequences of fisheries-induced selection is that the typical positive-size
selection by a trawl that catches both large juvenile and adult individuals induces
78 evolution of fast life histories (Andersen & Brander 2009; Laugen et al. 2014; Heino et
al. 2015). Fast life-histories can be characterized by fast juvenile growth, young age and
80 small size at maturation and high reproductive investment, which reduce post-
maturation growth rate and increase natural mortality. From a management

82 perspective, it is important to understand the population dynamical and social and
economic consequences of fisheries-induced evolution, to, if possible, design
84 management tools that minimize undesired evolutionary effects on outcomes valued by
humans, such as yield, recovery or the catch prospects of exceptionally large fishes
86 (Matsumura et al. 2011; Eikeset et al. 2013; Zimmermann & Jørgensen 2017).

88 Most empirical and theoretical research on phenotypic and evolutionary
changes caused by fisheries has focused on life-history traits (Devine et al. 2012; Heino
90 et al. 2015). Our understanding of fisheries-induced selection and potential for
evolutionary changes in traits other than life-history traits, such as behavioral or
92 physiological traits, is far less developed (Uusi-Heikkilä et al. 2008; Heino et al. 2015;
Arlinghaus et al. 2017). In particular, there is a gap in the knowledge related to the
94 potential for adaptive effects of fishing on behavioral traits in wild-living fish
populations. Arlinghaus et al. (2016, in press) recently proposed that wildlife hunting
96 and fishing may foster the evolution of a “timidity syndrome” where adapted
populations become shyer, less explorative, less aggressive, less active and/or less bold
98 due to a combination of learning within the realm of plasticity and evolution. Very few
on fisheries-induced evolution are available to support these predictions given the lack
100 of behavioural mechanisms present in most theoretical investigations on fisheries-
induced evolution. One exception is a study that included behavioral mechanisms in the
102 analysis of life-history evolution caused by fisheries found that elevated, yet
unselective, fishing mortality selected for bolder and/or more aggressive foraging

104 among juveniles (Jørgensen & Holt 2013). This finding is the opposite effect of the one
proposed by the “timidity syndrome”. However, the generality of the results by
106 Jørgensen and Holt (2013) is limited because no size or behavior-selective situations
were addressed. In another recent model, Mee et al. (2017) focused on studying the
108 evolution of movement rates in a spatially explicit framework in a sexual fish, but they
authors omitted corresponding selection acting on life-history traits. Given the limited
110 scope of previous models, it remains unclear what to expect when fishing not only acts
on size, but also on behavioral traits alone or in combination with size, as in most
112 fisheries (Arlinghaus et al. 2017; Diaz Pauli & Sih 2017).

114 A rich literature has shown that the behavior expressed by individual fish plays a
key role in exposing individuals to fishing gear (Pitcher 1995; Conrad et al. 2011;
116 Løkkeborg et al. 2014). However, the specific behaviors that may be under selection
depend on the species and the type of gear. Of relevance is whether the gear is passive,
118 such as gill-nets, traps, commercial long-lines and recreational angling with rod and line,
or active, such as trawling or seining. Most passive gear types have been found to select
120 for bold fishes, leaving behind shy individuals (reviewed in Arlinghaus et al. in press, see
also Monk and Arlinghaus 2017). For example, an experimental study by Diaz-Pauli et
122 al. (2015) in guppies (*Poecilia reticulata*) showed that traps selected for shy fishes (by
preferentially capturing bold fishes), while experimental trawls selected for bold fishes
124 (by preferentially capturing timid and social fishes). In another experimental study in
minnows (*Phoxinus phoxinus*), Killen et al. (2015) found that experimental trawls

126 captured fishes with small swimming ability, low basal metabolic rates and low
anaerobic scope. Fish with low basal metabolism and often also shy following ideas of
128 the pace-of-life hypothesis (Réale et al. 2010). Based on these findings, one can
reasonably assume that passive and active gear types systematically select for opposing
130 behavioural traits. Note, however, that the empirical research based on the relationship
of behavioural traits and vulnerability to active gears is much less well developed
132 compared to passive gear types (Diaz-Pauli and Sih in press). Consequently, it is not
clear that active gears will always preferentially select shy fishes, but it is safe to
134 assume that fisheries will be generally selective for both size and behavioral traits
(Allendorf & Hard 2009; Heino et al. 2015; Arlinghaus et al. 2017). We therefore
136 explored the whole “sphere of opportunities” in terms of selection acting on the
boldness-shyness axis with and without additional selection on size to understand the
138 direction and strength of selection on behaviour and life-history traits in a range of
contexts.

140

For fisheries-induced selection to operate on behavior, it is paramount that
142 behavioral traits are stable phenotypes that characterize individuals within populations.
A plethora of recent studies has revealed that fishes indeed reveal less plasticity in their
144 behaviors than previously believed, forming stable among-individual differences in
behavioral types (Conrad et al. 2011; Mittelbach et al. 2014). One of the key personality
146 traits in animals in general is boldness (Réale et al. 2007), which is often correlated with
other personality traits such as aggression, exploration, sociability or activity, thereby

148 creating behavioral syndromes (Sih et al. 2004). Behavioral traits are in turn often
correlated with physiological and life-history traits, resulting in an integrated phenotype
150 (pace-of-life hypothesis, Réale et al. 2010). For example, boldness (i.e., risk-taking
during foraging) has been shown to be correlated with traits associated with a fast-life
152 history (Wolf et al. 2007; Biro & Stamps 2008; Réale et al. 2010). Hence, life-history
traits such as growth rate may change due to direct selection operating on size or due
154 to indirect selection responses caused by direct selection on correlated behavioral traits
(Biro & Post 2008; Biro & Sampson 2015).

156

The question addressed here is what selection differentials and life-history
158 responses to expect when a fishery is either unselective, size-selective of various degree
or size- and boldness-selective. The baseline prediction is that an entirely unselective
160 fishery with respect to traits and states should lead to the evolution of a fast-life
history, which is associated with intensified foraging behavior (i.e., elevated boldness;
162 Jørgensen & Holt 2013). The reason is simply that intensified foraging allows the
individual to gain sufficient resources to achieve fast growth rate as juvenile to invest
164 early into reproduction and devote a large fraction of surplus energy into gonads
(Jørgensen and Holt 2013). Such effects should be magnified in a trawl-like fishery that
166 targets large, but possibly shy fishes (Diaz Pauli et al. 2015), if the behavioural selection
directly operates on shyness and not on other behavioural traits (e.g., schooling or
168 swimming ability). By contrast, in most passively operated fishing gears (e.g., traps or
angling) where the capture probability is usually both size (Kuparinen et al. 2009) and

170 boldness-related (Klefoth et al. 2012), evolution of a fast-life history with a timid
behavioral phenotype should be expected (Arlinghaus et al. 2016, in press). To examine
172 these predictions, we use a quantitative genetics calculation based on a size-based
model of fish life history (Andersen and Brander 2009). We included a similar
174 behavioral mechanism to the one used by Jørgensen and Holt (2013) and present the
first complete analysis of what selection responses to expect on fish behavioral traits
176 across a range of selectivities, representing a variety of gear types and possible
management tools directed at modifying which sizes of fishes can be retained (e.g.,
178 variants of size-based harvest limits).

Material & methods

180 The model estimates the evolutionary responses of three fundamental adaptive and
heritable traits: boldness τ , size at maturation w_m , and size-specific reproductive
182 investment k_r . The (fixed) population average of trait x is denoted by a bar: \bar{x} . The
selection differential $S(\bar{x})$ and the rate of evolutionary change in the average trait,
184 $d\bar{x}/dt$, are calculated using quantitative genetics as in Andersen and Brander (2009).
Changes in the three fundamental traits affect growth rate and asymptotic (maximum)
186 body size. The description of the model is divided into three parts: the life-history
model, the quantitative genetics calculations, and the determination of the fixed trait
188 values of the unexploited population.

190 Life-history model

The life-history model presented here is based on earlier work by some of us (Andersen & Brander 2009). It constitutes a complete description of individual growth, reproduction and survival. The model resolves the vital processes in an average individual as a function of its body size (represented by weight) w , and accounts for the trade-off between growth and reproduction (Roff 1983; Lester et al. 2004). Rates of maximum consumption, standard metabolism and natural mortality are assumed to scale with body weight following standard metabolic scaling rules (Brown et al. 2004). Consequently, maximum consumption and standard metabolism is proportional to w^n , where n is the metabolic exponent, and mortality is proportional to w^{n-1} . This way of linking the size-scaling of metabolism and mortality has support from size-spectrum theory, where the exponent $1 - n$ on mortality is a result of predation by predators whose need for food scale with exponent n (Sheldon et al. 1977; Andersen & Beyer 2006). We use the canonical value of the metabolic exponent $n = 3/4$ but examine the sensitivity of the results to this assumption. The values of the scaling exponents also have empirical support: metabolism and maximum consumption scales with $3/4$ for fish (Kjørboe & Hirst 2014), and mortality with exponent $-1/4$ (Peterson & Wroblewski 1984; Lorenzen 2000). We introduce the fundamental trade-off between consumption (leading to growth) and natural mortality (Stamps 2007) into our established model framework to explicitly consider behavioral dynamics and the fishing mortality due to increased risk of predation or exposure to gear while foraging.

212 Our description of the trade-off related to behaviour is inspired by the classic literature
on optimal foraging (Lima & Bednekoff 1999; Werner & Anholt 2014). Behaviour is
214 represented by a parameter $\tau \in [0: 1]$, which conceptually is the fraction of time the
individual spends foraging. While foraging in risky foraging arenas outside refuges
216 (Ahrens et al. 2012), the individual encounters food, but exposes itself to predation as it
typically observed (Lima & Dill 1990; Biro et al. 2005) and described by optimal foraging
218 theory (McNamara et al. 2001). Given this trade-off, the behavioral process in our
model is best described by boldness as personality trait, which is defined in modern
220 behavioural ecology as risk-taking during foraging (Réale et al. 2007). The trade-off
implies that bold individuals (those with high τ) will have higher consumption and faster
222 growth at the expense of higher predation mortality than timid individuals (low τ), for
which there is abundant empirical support (Biro et al. 2005; Biro & Post 2008;
224 Nakayama et al. 2017).

226 The trade-off between growth and mortality is assumed linear: an increasing foraging
activity implies a similar increase in predation risk. In reality the trade-off might be non-
228 linear, i.e. with relatively higher or lower mortality risk associated with increased
foraging activity. Here, we are only interested in selection responses and therefore only
230 the fitness gradient matters. The trade-off can therefore equally well be viewed as a
linearization of the trade-off around the current fixed trait value. It will therefore
232 matter little whether the trade-off is linear or non-linear.

234 In the following we show how the three fundamental traits, boldness τ , size at
 maturation w_m , and size-specific reproductive investment k_r , affect available energy,
 236 growth, reproduction, and ultimately mortality.

238 *Available energy*

A foraging individual encounters food with a rate τR_r where R_r is the encountered food
 240 (unit biomass per time). The assimilated energy can be described with a Holling
 functional response type II as

242

$$E_a = \epsilon_a C_m \frac{\tau R_r}{\tau R_r + C_m}, \quad (1)$$

244 where C_m is the maximum consumption rate and ϵ_a the assimilation efficiency. The
 maximum consumption rates scales with body weight w as $C_m = A_m w^n$, where A_m is a
 246 constant, n the metabolic exponent, and w the body weight. By defining $A = \epsilon_a A_m$ and
 $R = R_r / C_m$, the assimilated energy can be rewritten in a simpler form as:

248

$$E_a = A w^n \frac{\tau R}{\tau R + 1}. \quad (2)$$

250 Here R is the ratio between encountered food and what can be maximally be
 consumed. If $R > 1$ there is more food available than can be consumed and vice versa.

252 A value of $R \approx 1$ for a fully foraging individual ($\tau = 1$) corresponds to a predator

assimilating at half its assimilative capacity. Assimilation at less than half capacity is
 254 usually observed under field conditions (Armstrong & Schindler 2011), and we
 therefore assume $R = 1$, which with $\tau < 1$ leads to assimilation at less than half
 256 capacity.

258 *Growth and reproduction*

The consumed energy is used for standard metabolism $k_0 w^n$ and activity $k_a \tau w$, where
 260 the k 's are constants and the cost of activity is proportional to the boldness trait τ .
 Standard metabolism is assumed to scale with the same exponent as the maximum
 262 consumption ($n = 3/4$) while activity is proportional to weight, in accordance with
 calculations of optimal foraging (Ware 1978). The available energy (assimilated energy
 264 minus costs) then becomes

$$E = A w^n \frac{\tau R}{\tau R + 1} - k_0 w^n - \tau k_a w. \quad (3)$$

266

To simplify notation, we define the critical feeding level $f_c = k_0 w^n / (A_m w^n)$ as the
 268 ratio between standard metabolism and maximum consumption. This makes it possible
 to write available energy as

270

$$E = A \left(\frac{\tau R}{\tau R + 1} - f_c \right) w^n - \tau k_a w. \quad (4)$$

272 Reproductive investment is proportional to body mass as is typical for fish (Roff 1983),
 with a proportionality factor k_r . Maturation is described with a function that switches
 274 between 0 and 1 around the size at maturation, w_m :

$$\psi(w, w_m) = \left(1 + \left(\frac{w}{w_m}\right)^{-10}\right)^{-1}. \quad (5)$$

276
 Growth can then be determined as the remaining available energy after reproduction in
 278 adults:

$$g(w) = A \left(\frac{\tau R}{\tau R + 1} - f_c \right) w^n - (\tau k_a - \psi(w, w_m) k_r) w. \quad (6)$$

280
 As in Andersen and Beyer (2015), we assume that energy is divided between
 282 reproduction k_r and activity k_a with a constant fraction ϵ_a . This means that $k_a =$
 $k_r \epsilon_a / (1 - \epsilon_a)$. The asymptotic (maximum) size W is reached when somatic growth is
 284 zero, i.e., $g(W) = 0$:

$$W = \left[A \left(\frac{\tau R}{\tau R + 1} - f_c \right) \frac{1}{\tau k_a + k_r} \right]^{\frac{1}{1-n}} \quad (7),$$

286
 which shows that asymptotic size will decrease if investments in reproduction k_r are
 288 increased and typically increase if boldness increases (Figure 1).

290 *Mortality*

Survival from one size w_a to another size w_b is found as the solution to $dP/dt =$

292 $-\mu(w)$ which is:

$$294 \quad P_{w_a \rightarrow w_b} = \exp\left[-\int_{w_a}^{w_b} \frac{\mu(w)}{g(w)} dw\right] \quad (8),$$

296 where $\mu(w)$ is the mortality with contributions from predation and fishing.

298 Predation mortality μ_p declines with size $\propto w^{n-1}$ as is typical for fish (Peterson &

Wroblewski 1984; Lorenzen 2000) and is assumed proportional to boldness τ :

300

$$\mu_p = \alpha_p \tau w^{n-1} \quad (9).$$

302 Therefore, increased foraging activity by individuals with higher boldness τ leads to

increased predation mortality (as in Jørgensen and Holt 2013). The parameter α_p

304 describes the overall level of predation mortality.

306 Fishing is assumed to be unselective or selecting solely on size, solely on boldness or

jointly on size and boldness/shyness. The size-selective term is described by a sigmoidal

308 curve (typical for trawling and long-lining, Myers & Hoenig 1997), switching from zero

to one around a size w_F . Variation in mesh sizes or changes in allowable landing size

310 (e.g., minimum or maximum-length limit or the combination, a harvest slot) alters size-
 selectivity (Jørgensen et al. 2009; Matsumura et al. 2011; Mollet et al. 2016) and is
 312 simulated by changing w_F (Figure 2a). To simulate a harvest slot fishery (not to be
 confused with a protected slot-fishery) where only a certain intermediate size-range is
 314 targeted (as is common in gill-nets) the selectivity may again go down to zero at a size
 w_{FF} (here taken to be 10 times larger than the size where fishing starts) (Figure 2b). The
 316 selection on behavior is assumed proportional to boldness, switching around the fixed
 trait value $\hat{\tau}$ with a steepness b_F (Figure 2c). Taken together the fishing mortality μ_F
 318 then becomes:

$$\mu_F(w, \tau) = F_0 \psi(w, w_F) (1 - \psi(w, w_{FF})) (1 + b_F(\tau - \bar{\tau})), \quad (10)$$

320 where F_0 is the overall fishing mortality, and the dimensionless parameter b_F describes
 322 the selection on boldness. Since we only need to evaluate derivatives of μ_F with respect
 to τ around $\bar{\tau}$ we will not obtain negative values of μ_F . The function ψ is the same that
 324 is used to describe maturation around the size at maturation w_m . Here it describes how
 selection changes from zero to full selection at the size w_F and back again to zero at the
 326 size w_{FF} . Assuming that selection on boldness by fishing is the same as the boldness-
 induced predation mortality corresponds to a value of $b_F = 1$. However, we also
 328 explore other scenarios of boldness selection, including negative selection where
 bolder individuals are better at escaping fishing gear as per the research by Diaz-Pauli
 330 et al. (2015). The four cases examined further are: 1) random harvest; only elevated

fishing mortality; 2) only size-selective harvest (w_F and w_{FF} varied; $b_F = 0$); 3) only
 332 boldness-selective harvest ($w_F = 0$, $w_{FF} = \infty$, b_F varied around 1); and 4) both size-
 and boldness-selective harvest (all parameters are non-zero). A base-case for the size-
 334 selectivity is trawl-like fishing in commercial fisheries, which is conceptually similar to
 exploitation with a minimum-length limit typical in recreational fisheries (positive size-
 336 selection) with $F_0 = 0.3 \text{ yr}^{-1}$, $w_F = 0.05W$ and $w_{FF} = \infty$ (Figure 2a).

338 Quantitative genetics

Responses to selection depend on the selection differential S , which is the mean
 340 change in the trait before and after selection (Matsumura et al. 2012). The selection
 differential is also proportional to the gradient of the life-time reproductive output
 342 evaluated around the mean of the fixed trait \bar{x} (Andersen et al. 2007):

$$S(\bar{x}) = \sigma_x^2 \frac{1}{R_0(x)} \frac{\partial R_0(x)}{\partial x} \Big|_{x=\bar{x}}, \quad (11)$$

344

where σ_x is the standard deviation of the variation of the trait in the population and the
 346 life-time reproductive output is found by integrating individual output multiplied by the
 survival from egg weight $w_{egg} \approx 1 \text{ mg}$ to asymptotic size:

348

$$R_0 \propto k_r \int_{w_{egg}}^W P_{w_{egg} \rightarrow w} \psi(w, W) w \, dw. \quad (12)$$

350 The constant of proportionality is immaterial because it vanishes when the ratio
 between the derivative and the value of R_0 is formed during the calculation of the
 352 selection differential.

354 In a natural population unaffected by fishing the selection differential is expected to be
 zero. However, with given the chosen parameters that was not the case for the traits
 356 size at maturation and reproductive investment, meaning that these traits were not in
 an evolutionarily stable state prior to the commencement of fishing. To address this, we
 358 calculate the relative selection differential S_{fish} due to the selective force from fishing
 as the difference between the selection responses with and without fishing:

360

$$S_{\text{fish}}(\bar{x}) = S(\bar{x}, F_0 \neq 0) - S(\bar{x}, F_0 = 0). \quad (13)$$

362 We choose two variants of normalized selection strength to compare selection on the
 three adaptive traits. We first calculated the mean-standardized selection gradient
 364 (which is perhaps the most suited measure of strength of selection to compare across
 traits different in mean and variance) and second the proportional selection response.

366

The mean-standardized selection gradient is given as (Matsumura et al. 2012):

368

$$\beta_{\mu}(\bar{x}) = \frac{1}{\bar{x}} \left(\frac{\bar{x}}{\sigma_x} \right)^2 S_{\text{fish}}, \quad (14)$$

370

which has dimensions of 1/generation and represents a fitness elasticity. σ_x/\bar{x} is the
 372 coefficient of variation (CV) of the trait. For simplicity, we choose identical CVs for the
 three traits examined.

374

The proportional selection response is the rate of change normalized by the trait value
 376 itself, while accounting for the heritability of the trait. It follows from the selection
 differential as:

378

$$r(\bar{x}) = \frac{h^2}{\bar{x}} S_{\text{fish}} \quad (15)$$

380 where $h^2 = 0.2$ is the (realistically moderate, compare Mousseau & Roff 1987;
 Dickerson et al. 2005; Thériault et al. 2007) heritability of each of the three traits. Note
 382 that the heritability of behavioural traits is often much higher than 0.2 (Dickerson et al.
 2005; Dochtermann et al. 2015), such that our model predictions underestimate the
 384 evolvability of behavioural traits compared to life-history traits. In the final results, we
 only report the proportional selection response because the two measures are
 386 proportional when the heritability is identical on all traits (Matsumura et al. 2012; eq.
 7):

388

$$r(\bar{x}) = h^2 \left(\frac{\sigma_x}{\bar{x}} \right)^2 \beta_{\mu}, \quad (16)$$

390 and with the parameters used (Table 1) the constant of proportionality is 0.008. To
 obtain the values in units of per year, the mean-standardized selection gradient and the
 392 selection response are divided by the generation time, approximated as the age of
 maturation.

394

Parameter values

396 The mean values of the three fundamental traits, boldness τ , reproductive investment
 k_r and size at maturation w_m , must be defined at the onset. The value of boldness in
 398 the absence of fishery $\bar{\tau}$ is assumed to be the one that optimizes R_0 . We calculate this
 numerically by finding the value of τ that gives the highest value of R_0 . The value of the
 400 mean reproductive investment k_r effectively determines the asymptotic size via eq. (7).
 We use k_r to conceptually represent different species of fishes, but report results as a
 402 function of asymptotic size. Finally, the size at maturation w_m is assumed proportional
 to asymptotic size; $w_m = \eta_m W$. This does not imply that w_m and k_r are directly
 404 correlated through the calculation of W with eq. (7); this relation is only used to
 calculate the starting value in the absence of fishing and not in the process of
 406 calculating selection responses. The values of the other parameters of the model are
 given in Table 1.

408

The model is solved numerically by discretizing the weight-axis in 1000 logarithmically
 410 spaced size bins, as described in Andersen & Beyer (2015, app. C).

Results

412 The predicted evolution in the four cases of selectivity patterns (1: random harvest; 2:
only size-selective harvest; 3: only boldness-selective harvest; 4: both size- and
414 boldness-selective harvest) on the three fundamental traits examined here (Figure 3).

416 The first two cases – random harvest and size-selectivity with a trawl-like selectivity
pattern – confirms that harvesting leads to the evolution of a fast-life history
418 characterized by reduced size at maturation and increased investment in reproduction.
Clearly, the effects of added mortality late in life, where the mortality is large compared
420 to natural mortality, dominates over the effect of added mortality early in life where
the mortality is much smaller than the natural mortality (Figure 2). Regarding boldness,
422 both cases leads to evolution of bolder individuals, and the rate of evolution on the
boldness trait is much faster than the selection on the life-history traits. Evolution of
424 increased boldness therefore occurs even if fishing gear selects neutrally with respect
to boldness. The optimum for the boldness trait before selection is the result of a
426 balance between the benefit of the faster growth that results from higher boldness and
the costs of increased predation risk. When mortality is elevated regardless of the
428 boldness, this balance shifts in the direction where the cost of predation mortality
becomes less compared to the total mortality. This generates a selection response
430 towards increased boldness. The effect is further compounded by the increased
investment in reproduction that comes at the cost of reduced adult growth, which can
432 be compensated by the higher consumption of bolder individuals. Finally, increased

mortality increases the pressure to ensure survival to maturation to ensure at least one
434 spawning event. This is facilitated by faster juvenile growth.

436 Fishing gear selecting on boldness traits, either solely (case 3) or in conjunction with
size-selectivity (case 4), has the same selection responses on size at maturation and
438 reproductive investment as without selection for boldness, i.e., fast life-histories are
favored. The main outcome of selection on boldness is an additional selection response
440 towards more timid individuals, leading to a weakening of the selection on boldness. If
the selection on boldness is increased ($b_F > 1$) then then the selection response on the
442 personality trait is completely reversed, and instead of selecting for bolder individuals,
there is now selection for more timid individuals (Figure 4b). The reason is simply that
444 now there is an increasing cost to be bold by elevating the chances of being captured,
which reverses and sharply reduces the evolution of fish boldness in our model. While
446 this outcome is fairly intuitive, it is less obvious, yet in line with expectations, why the
absence of selection on boldness leads to increased boldness (case 1 and 2).

448
The selection responses are roughly proportional to the fishing mortality and, for
450 boldness, to the selection strength acting on boldness (Figure 4). The order of
magnitude of the selection responses of the three traits are roughly 0.1 % per year. The
452 selection responses of timidity only exceed the selection responses of the two other
traits when selection on boldness is exceedingly large (parameter b_F) (Figure 4b). By

454 contrast, when timid fish are more likely to be captured (negative values of b_F in Figure
4b), evolution of boldness occurs also under size- and timidity-selective fisheries.

456

Changes in growth and asymptotic size

458 The combined effects of the selection responses of the three adaptive traits
(maturation size, investment in reproduction and boldness) are summarized in the
460 impact of fishing on size-at-age and asymptotic size (Figure 5). In the cases without
selection on boldness, the effects of evolution of boldness (leading to faster growth)
462 and increased investment in reproduction (leading to slower growth) cancel one
another, and growth is largely unchanged. This result was anticipated by Eq. (7). Clearly,
464 boldness-selectivity in addition to mere size-selectivity has the potential for a magnified
change in growth rate leading to a reduction in asymptotic size, in particular for small-
466 bodied fish species.

468 While the result that selecting bolder individuals leads to evolution of more timid
individuals (cases 3 and 4) can be understood intuitively, there are two aspects of the
470 results which are less intuitive: *i)* why does selection on boldness not affect the
direction of the selection responses of life history traits? *ii)* why does random and trawl
472 selectivity (cases 1 and 2) lead to the same selection responses on the life history traits
(reproductive investment and size at maturation)? Regarding the first question, the
474 reason lies in the life-time reproductive output being only influenced by the level of
mortality imposed, not whether it is selective on boldness or not. The level of mortality,

476 and thus the level of selection, is only affected when differences in boldness are
considered. We can understand the answer to *ii*) by examining the effects of size
478 selection, as we do next.

480 *Sensitivities in response to altered size-selectivity patterns*

The selection responses depend on the size-selectivity imposed by the fishery as
482 described by size of 50 % selection relative to asymptotic size η_F (Figure 6). Most
importantly, a shift is seen in when selection changes from targeting both juveniles and
484 adults to when only adult are targeted ($\eta_F W > \text{size at maturation}$) (Figure 6a). When
only adults are targeted the strength of selection declines and the sign of the selection
486 response on boldness changes as the minimum-size limit in the trawl-like selectivity
moves up. Selecting only large mature individuals thus is expected to induce timidity,
488 while selecting smaller fishes (including juveniles) selects for boldness when the fishery
is entirely size-selective. The reason for this change is that as mortality is decreased on
490 adults it becomes less important to grow fast, and the push towards increased boldness
diminishes. When juveniles are also selected ($\eta_F \ll \text{size at maturation}$), the selection
492 responses on the life history traits become independent on the size at selection. This is
likely because for these small sizes natural mortality, which declines with body size, is
494 higher than the fishing mortality, and the effect of the elevated fishing has less selective
power. This is the reason why random selection and size-specific selection have similar
496 effects. As before, selection for boldness when the size-selectivity targets also juveniles
or small adults is entirely reversed (i.e., timid fish are favoured) when there is also

498 boldness-selectivity common to many passive fishing gears (Figure 6b). The selection on
life-history traits with elevation of minimum-length limits works as before, i.e., direct
500 selection on boldness does not alter the life-history responses of a fast life-history, but
the evolutionary response is reduced if only very large adults are targeted.

502

Gill-net selectivity (which resembles management in recreational fisheries using a
504 harvest slot) leads to more complex selection responses, but does not avoid selection
on the three traits (Figure 6c+d). The results are similar to the trawl selectivity pattern
506 when the gill-net only harvests mature individuals. In that case, there is no selection on
boldness, and only reproductive investment is predicted to rise (Figure 6c). However,
508 compared to the trawl-like fishery (Figure 6a) the life-history responses and the
evolution of boldness are overall reduced (particularly in relation to boldness evolution)
510 when fishing using a harvest slot only selects juvenile individuals (Figure 6c). The
lowered selection responses on all three traits is particularly visible when selection
512 operates on both size and boldness (Figure 6d). Then, although under a gill net
selectivity, evolution of timidity is predicted when the slot targets mature fishes.
514 Selection responses with gill net selectivity are overall lower compared to a trawl-like
selectivity because the cumulative mortality, i.e. the mortality summed over the whole
516 size range, is smaller at a given fishing mortality rate when only a limited size range is
selected compared to the range selected by a trawl.

518

Sensitivity to changes in fundamental parameters

520 The model relies on the nine parameters in Table 1 (k_r is a free parameter that
determines the asymptotic size). Selection responses are directly proportional to the
522 heritability h^2 and to the C.V. of the traits σ_x/\bar{x} . This follows directly from Eqs. (11) and
(15). These parameters therefore only affect the absolute magnitude of the selection
524 responses prediction and do not affect the qualitative results of the different selection
scenarios. The sensitivity of the selection responses to the other 7 parameters are
526 explored in Figure 7. The selection responses on the three traits are remarkable
insensitive to changes in most parameters. Even changing the metabolic exponent n
528 has a small effect. While the traits themselves are relatively insensitive to changes in
the parameter values, the asymptotic size is more sensitive. We therefore conclude
530 that the predictions on changes in the traits, including boldness, are relatively robust to
parameter choices, while the predictions on changes in asymptotic size are less robust
532 and might vary more between species than predicted by the model.

Discussion

534 The model replicates earlier model studies showing that increased mortality by fishing
selects for individuals with a fast life history with earlier maturation and higher
536 reproductive investment. This result emerges regardless of whether selection was size
selective or boldness selective. Increased mortality by fishing favours early-maturing
538 individuals at small size, which have a chance to reproduce before being caught.
Similarly, individuals that invest more in reproductive output early in life are better off
540 because the likelihood of a future spawning event is greatly diminished when mortality

rate increases due to fishing. These results are well-known from life-history theory
542 (Stearns 1992), evolutionary fisheries models of various structure (Arlinghaus et al.
2009; Poos et al. 2011; Dunlop et al. 2015a), laboratory experiments with model fish
544 species (Uusi-Heikkilä et al. 2015) and from time-series analysis of phenotypic field data
of harvested natural populations (Jørgensen et al. 2007; Devine et al. 2012; Heino et al.
546 2015). We demonstrate that selection on boldness can have strong additional impacts
on growth rate and asymptotic size. Selection on boldness has the potential to either
548 enhance or mitigate the selection on growth rate depending on whether fisheries
selection is mainly directed at boldness (enhanced response) or whether it acts on top
550 of size-selection (mitigated response). Our work thus underscores Biro and Post's
(2008) and Biro and Sampson's (2015) reasoning that any observed changes in growth
552 rate may be caused by direct selection on boldness rather than being caused by size-
selection or by life-history adaptation to elevated mortality alone.

554

As a further new finding we show that we can expect boldness to either increase or
556 decrease depending on the degree of selection acting on behavioral traits. Based on our
findings, elevated, but random mortality favors boldness (as in the model of Jørgensen
558 and Holt 2013), whereas direct selection on boldness alone or in addition to size-
selection favors timidity, qualitative corresponding to the hypothesis by Arlinghaus et
560 al. (2016, in press). In passively operated fishing gear, vulnerability to capture is likely
strongly and often mainly boldness-driven (Klefoth et al. 2012; Biro & Sampson 2015),
562 which is why one can expect changes in growth rate and evolution of timidity

particularly in reaction to exploitation by gill nets, traps or hook-and-line. It will be
564 important to test this clear-cut prediction in the future in empirical settings, because
increased timidity will have substantial effects on catchability and hence on stock
566 assessment, fisher well-being and effectiveness of management tools such as protected
areas (Januchowski-Hartley et al. 2011; Alós et al. 2016; Arlinghaus et al. 2017).

568

Evolution of behavior

570 Selection on boldness has the potential to somewhat mitigate the selection response
towards a faster life history by inducing timidity and thus slower juvenile growth rates.
572 It does, however, not change the selection on size at maturation and investment in
reproduction. However, if timid fish are selectively captured (as might be the case in
574 some active gear types; Diaz-Pauli et al. 2015; Killen et al. 2015), evolution of boldness
is also predicted under size- and boldness selective fisheries. How a given fishery selects
576 on boldness depends on the nature of the fishing operation in relation to species-
specific behavioral patterns and life-styles, which constitutes a much needed research
578 area for the future (Heino et al. 2015; Arlinghaus et al. in press; Diaz-Pauli and Sih in
press). Before that research becomes available, we can tentatively propose that
580 because passive gears, such as a gill nets, traps, or hooks, require individuals to actively
enter the gear, these gears should preferentially target bold individuals and hence
582 select for elevated timidity (the “timidity syndrome”, Arlinghaus et al. 2016, in press).
How active gear, such as trawl or purse seines, targets different behavioral types is less
584 known, but if they preferentially target timid individuals (Diaz-Pauli and Sih in press),

586 according to our model they will select for bold individuals, amplifying the selection
588 responses induced by elevated mortality and leading to even faster life histories and
590 strongly elevated natural mortality (Jørgensen and Holt 2013). However, trawls might
592 also select on other personality traits such as swimming activity or sociability or
594 physiological traits such as metabolic scope and ability for sustained swimming (Diaz-
596 Pauli et al. 2015; Killen et al. 2015) – traits not considered in our model. Similarly, there
is evidence that other active gear types such as spear guns favor less explorative and
timid individuals rather than bold ones (Januchowsky-Hartley et al. 2011), suggesting
that not all active gear types preferentially exploit shy fishes. Without a dedicated
model that considers a range of behavioural traits and their correlations, it is very hard
to come up with precise predictions about which behaviours will exactly change in trawl
and other active gear-type fisheries. Future theoretical and empirical research is
needed in this underexplored area.

598

Model limitations

600 The changes in three fundamental life-history and behavioural traits (size at
602 maturation, investment in reproduction and boldness) were found to lead to changes in
adult growth rate and a reduction in asymptotic size, which is a classical prediction
about the consequences of fisheries-induced evolution (Jørgensen et al. 2007, Laugen
604 et al. 2014). However, we find that the prediction on changes in asymptotic size is at
the same time fairly uncertain, as it relies on the value of the parameter ϵ_A that
606 describes the partitioning of energy between activity and reproduction, which is not

well known empirically (Andersen & Beyer 2015). Changes in asymptotic size may also
608 be driven by changes in allocation to reproduction during ontogeny, which is
unresolved by the model. Instead, we have assumed that allocation to reproduction is
610 directly proportional to individual size, as is customary in many life-history models,
however, if allocation increases faster than proportional with size (Edeline et al. 2007;
612 Quince et al. 2008) more energy will be allocated to reproduction in larger individuals,
and the reductions in asymptotic size will be even stronger than we predict.
614 Importantly, however, the downsizing of adults is reduced if behavior is considered
under selection in addition to size, which will be the default case in many fisheries (Biro
616 and Post 2008; Uusi-Heikkilä et al. 2008; Arlinghaus et al. in press). Therefore,
evolutionary costs while considering behavior with respect to size are smaller from an
618 adult size (and likely yield) perspective than assumed before in life-history models that
omit behavioral dynamics. Importantly, a recent experimental harvesting experiment in
620 zebrafish (*Danio rerio*) that strongly selected on size found evolution of timidity and at
the same time only subtle changes in terminal size and no evolution of juvenile growth
622 rate (Uusi-Heikkilä et al. 2015), agreeing with our findings.

624 Another limitation of our modelling approach is the absence of population regulation
through density-dependent processes, which is a key ingredient of alternative
626 individual-based eco-genetic models of fisheries-induced evolution (Dunlop et al.
2015b; Eikeset et al. 2016). A previous modelling study that examined the impact of a
628 range of density-dependent processes acting on fecundity and mortality on selection

differentials on reproductive investment in pike (*Esox lucius*) (Arlinghaus et al. 2009)
630 indeed found that the predictions were rather sensitive to density-dependent somatic
growth but insensitive to density-dependent mortality. However, the sign of the
632 selection differentials on reproductive investment remained identical whether density-
dependence was acting on growth or not. Moreover, the key predictions emerging from
634 our stylized model were roughly similar to the predictions of more complex eco-genetic
models in terms of the expected evolution of fast life histories under most situations in
636 fisheries (Eikeset et al. 2013; Dunlop et al. 2015b). Nevertheless, it is clear that our
work shall be extended and replicated with other model frameworks to analysis its
638 stability. Further, our model assumes that the entire stock is only exposed to one gear
type selectivity. Our findings do not hold for mixed gear situations, which demand
640 careful calibration to actually selection pressures caused by varying gear and the
modelling of spatial gene flow. The scope of our work is beyond this, but some recent
642 work has started to look at spatial explicit models (Mee et al. 2017). Finally, it is
important to consider multi-species contexts in future evolutionary models and a range
644 of behavioural traits that are either correlated with each other forming behavioural
syndromes (Sih et al. 2004) or independently affecting vulnerability to capture and
646 resource intake (e.g., boldness and activity or space use). Empirical research is needed
to provide the data about correlations among traits to inform such models. Until that
648 research becomes available our predictions on the relative impact of size-selectivity and
boldness-selectivity represents the best possible estimates, and they were found to be
650 independent of specific assumptions and size-selectivity of fishing. Our results on the

magnitudes of evolutionary rates, however, are more uncertain as they depend on
652 exact values of parameters. Least robust are our predictions on changes in asymptotic
size. Moreover, our findings on the relative impacts of gill net selectivity confounded
654 effects stemming from altered size-selection with altered effective exploitation rates
(not the case in Mollet et al. 2016), warranting further study in the future.

656

Consequences

658 Based on our current knowledge, we propose that predicting the evolutionary
consequences of fisheries for populations will benefit from explicit consideration of
660 behavioral dynamics. In the absence of more detailed knowledge, it is possible that
active gear that targets timid individuals (Diaz-Pauli and Sih in press) will select for
662 bolder fishes. This result is valid even in the absence of direct selection on boldness, but
will be even stronger if timid fishes are preferentially captured (as might be the case in
664 active gear types Diaz-Pauli et al. 2015). Conversely, passive gear is more robustly
known to target bold individuals (which often have faster life histories, Réale et al.
666 2010), thereby evolutionarily favoring increased timidity. Many commercial and
recreational fisheries operate with passive gear – long lining for pelagic top predators in
668 the ocean, gill netting in coastal areas or recreational fishing of freshwater lakes. It is
conceivable that a century of such fishing has created shyer individuals with lower
670 consumption rates and more risk averse life-styles, which may in turn translate to
reduced parental care in species providing this care (Sutter et al. 2012). This likely has
672 consequences for social groups, populations and food webs (Arlinghaus et al. in press;

Diaz-Pauli and Sih in press), and we also predict systematic erosion of catchability
674 through evolution of timidity (Alós et al. 2015; Philipp et al. 2015; Tsuboi et al. 2016)
largely independent of which harvest regulations (minimum-size limits, maximum-size
676 limit or harvest slot) are put in place. This is a major difference to previous studies who
found that life-history responses to fishing mortality can well be addressed by cutting
678 fishing mortality and changing selectivity patterns to a dome-shaped selectivity typical
of harvest slots and gill nets (e.g., Jørgensen et al. 2009; Matsumura et al. 2011;
680 Zimmermann & Jørgensen 2017). Our work instead suggests that evolution of timidity
by passive gear cannot be avoided unless the harvest slot leads to an exclusive removal
682 of juveniles, which is uncommon in most fisheries but indeed reported from selected
recreational fisheries (e.g., in shore recreational fisheries in Florida).

684
Importantly, because evolution in boldness, in either direction, will erode the index
686 value of fishery-dependent data by changing catchability over time, and have
potentially have large community and food web as well as managerial and fisheries
688 consequences (Arlinghaus et al. in press), we (and others, Diaz-Pauli and Sih in press)
suggest increasing attention to the possibility of fisheries shaping the mean and
690 variance of behavioral expressed by exploited fishes in nature.

692 **Acknowledgement**

KHA and LM were supported by the Centre for Ocean Life, a VKR Centre of Excellence
694 funded by the Villum Foundation. RA thanks Leander Höhne for editorial assistance.

696 **References**

- Ahrens RNM, Walters CJ, Christensen V (2012) Foraging arena theory. *Fish Fish* 13:41–
698 59
- Allendorf FW, Hard JJ (2009) Human-induced evolution caused by unnatural selection
700 through harvest of wild animals. *106:9987–9994*
- Alós J, Palmer M, Balle S, Arlinghaus R (2016) Bayesian state-space modelling of
702 conventional acoustic tracking provides accurate descriptors of home range
behavior in a small-bodied coastal fish species. *PLoS One* 11:e0154089
- 704 Alós J, Palmer M, Trías P, Díaz-Gil C, Arlinghaus R (2015) Recreational angling intensity
correlates with alteration of vulnerability to fishing in a carnivorous coastal fish
706 species. *Can J Fish Aquat Sci* 72:217–225
- Andersen KH, Beyer JE (2006) Asymptotic size determines species abundance in the
708 marine size spectrum. *Am Nat* 168:54–61
- Andersen KH, Beyer JE (2015) Size structure, not metabolic scaling rules, determines
710 fisheries reference points. *Fish Fish* 16:1–22
- Andersen KH, Brander K (2009) Expected rate of fisheries-induced evolution is slow.
712 *Proc Natl Acad Sci USA* 106:11657–11660
- Andersen KH, Farnsworth KD, Thygesen UH, Beyer JE (2007) The evolutionary pressure
714 from fishing on size at maturation of Baltic cod. *Ecol Modell* 204:246–252
- Arlinghaus R, Alós J, Klefoth T, Laskowski K, Monk CT, Nakayama S, Schröder A (2016)
716 Consumptive tourism causes timidity, rather than boldness, syndromes: A
response to Geffroy et al. *Trends Ecol Evol* 31:92–94

- 718 Arlinghaus R, Laskowski K, Alos J, Klefoth T, Monk CT, Nakayama S, Schröder A (2017)
 Passive gear-induced timidity syndrome in wild fish populations and its potential
 720 ecological and managerial implications. *Fish Fish* 18(2) 360-373.
- Arlinghaus R, Matsumura S, Dieckmann U (2009) Quantifying selection differentials
 722 caused by recreational fishing: development of modeling framework and
 application to reproductive investment in pike (*Esox lucius*). *Evol Appl* 2:335–355
- 724 Armstrong JB, Schindler DE (2011) Excess digestive capacity in predators reflects a life
 of feast and famine. *Nature* 476:84–87
- 726 Beverton RJH (1992) Patterns of reproductive strategy parameters in some marine
 teleost fishes. *J Fish Biol* 41:137–160
- 728 Biro PA, Post JR (2008) Rapid depletion of genotypes with fast growth and bold
 personality traits from harvested fish populations. *Proc Natl Acad Sci U S A*
 730 105:2919–2922
- Biro PA, Post JR, Abrahams M V. (2005) Ontogeny of energy allocation reveals selective
 732 pressure promoting risk-taking behaviour in young fish cohorts. *Proc R Soc London*
B Biol Sci 272:1443–1448
- 734 Biro PA, Sampson P (2015) Fishing directly selects on growth rate via behaviour:
 implications of growth-selection that is independent of size. *Proc R Soc B* 282:13–
 736 15
- Biro PA, Stamps JA (2008) Are animal personality traits linked to life-history
 738 productivity? *Trends Ecol Evol* 23:361–368
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory

- 740 of ecology. *Ecology* 85:1771–1789
- Conrad JL, Weinersmith KL, Brodin T, Saltz JB, Sih A (2011) Behavioural syndromes in
742 fishes: A review with implications for ecology and fisheries management. *J Fish Biol*
78:395–435
- 744 Devine JA, Wright PJ, Pardoe HE, Heino M (2012) Comparing rates of contemporary
evolution in life-history traits for exploited fish stocks. *Can J Fish Aquat Sci*
746 69:1105–1120
- Diaz Pauli B, Sih A (2017) Behavioural responses to human-induced change: Why fishing
748 should not be ignored. *Evol Appl*:in press
- Diaz Pauli B, Wiech M, Heino M, Utne-Palm AC (2015) Opposite selection on
750 behavioural types by active and passive fishing gears in a simulated guppy *Poecilia*
reticulata fishery. *J Fish Biol* 86:1030–1045
- 752 Dickerson BR, Willson MF, Bentzen P, Quinn TP (2005) Heritability of life history and
morphological traits in a wild pink salmon population assessed by DNA parentage
754 analysis. *Trans Am Fish Soc* 134:1323–1328
- Dieckmann U, Heino M (2007) Probabilistic maturation reaction norms: Their history,
756 strengths, and limitations. *Mar Ecol Prog Ser* 335:253–269
- Dochtermann NA, Schwab T, Sih A (2015) The contribution of additive genetic variation
758 to personality variation: heritability of personality. *Proc R Soc London B Biol Sci*
282:20142201
- 760 Dunlop ES, Eikeset AM, Stenseth NC (2015a) From genes to populations: How fisheries-
induced evolution alters stock productivity. *Ecol Appl* 25:1860–1868

- 762 Dunlop ES, Eikeset AM, Stenseth NC (2015b) From genes to populations: how fisheries-
induced evolution alters stock productivity. *Ecol Appl* 25:1860–1868
- 764 Edeline E, Carlson SM, Stige LC, Winfield IJ, Fletcher JM, James J Ben, Haugen TO,
Vøllestad LA, Stenseth NC (2007) Trait changes in a harvested population are
766 driven by a dynamic tug-of-war between natural and harvest selection. *Proc Natl
Acad Sci U S A* 104:15799–804
- 768 Eikeset AM, Dunlop ES, Heino M, Storvik G, Stenseth NC, Dieckmann U (2016) Roles of
density-dependent growth and life history evolution in accounting for fisheries-
770 induced trait changes. *Proc Natl Acad Sci* 113:201525749
- Eikeset AM, Richter A, Dunlop ES, Dieckmann U, Stenseth NC (2013) Economic
772 repercussions of fisheries-induced evolution. *Proc Natl Acad Sci U S A* 110:12259–
64
- 774 Hartvig M, Andersen KH, Beyer JE (2011) Food web framework for size-structured
populations. *J Theor Biol* 272:113–122
- 776 Heino M, Díaz Pauli B, Dieckmann U (2015) Fisheries-Induced Evolution. *Annu Rev Ecol
Evol Syst* 46:461–480
- 778 Januchowski-Hartley FA, Graham NAJ, Feary DA, Morove T, Cinner JE (2011) Fear of
fishers: human predation explains behavioral changes in coral reef fishes. *PLoS*
780 *One* 6:e22761
- Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS, Brander K, Ernande B,
782 Gårdmark AG, Johnston F, Matsumura S, Pardoe H, Raab K, Silva A, Vainikka A,
Dieckmann U, Heino M, Rijnsdorp AD, Gardmark A, Johnston F, Matsumura S,

- 784 Pardoe H, Raab K, Silva A, Vainikka A, Dieckmann U, Heino M, Rijnsdorp AD (2007)
Managing evolving fish stocks. *Science* 318:1247–1248
- 786 Jørgensen C, Ernande B, Fiksen Ø (2009) Size-selective fishing gear and life history
evolution in the Northeast Arctic cod. *Evol Appl* 2:356–370
- 788 Jørgensen C, Holt RE (2013) Natural mortality: Its ecology, how it shapes fish life
histories, and why it may be increased by fishing. *J Sea Res* 75:8–18
- 790 Killen SS, Nati JH, Suski CD (2015) Vulnerability of individual fish to capture by trawling
is influenced by capacity for anaerobic metabolism. *Proc Biol Sci* 282:20150603
- 792 Kjørboe T, Hirst AC (2014) Shifts in mass-scaling of respiration, feeding, and growth
rates across life-form transitions in marine pelagic organisms. *Am Nat*
- 794 Klefoth T, Skov C, Krause J, Arlinghaus R (2012) The role of ecological context and
predation risk-stimuli in revealing the true picture about the genetic basis of
796 boldness evolution in fish. *Behav Ecol Sociobiol* 66:547–559
- Kuparinen A, Kuikka S, Merilaa J (2009) Estimating fisheries-induced selection:
798 Traditional gear selectivity research meets fisheries-induced evolution. *Evol Appl*
2:234–243
- 800 Laugen AT, Engelhard GH, Whitlock R, Arlinghaus R, Dankel DJ, Dunlop ES, Eikeset AM,
Enberg K, Jørgensen C, Matsumura S, Nusslé S, Urbach D, Baulier LC, Boukal DS,
802 Ernande B, Johnston FD, Mollet F, Pardoe H, Therkildsen NO, Uusi-Heikkilä S,
Vainikka A, Heino M, Rijnsdorp AD, Dieckmann U (2014) Evolutionary impact
804 assessment: Accounting for evolutionary consequences of fishing in an ecosystem
approach to fisheries management. *Fish Fish* 15:65–96

- 806 Lester NP, Shuter BJ, Abrams PA (2004) Interpreting the von Bertalanffy model of
somatic growth in fishes: the cost of reproduction. Proc R Soc London B 271:1625–
808 1631
- Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator
810 behavior: The predation risk allocation hypothesis. Am Nat 153:649–659
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review
812 and prospectus. Can J Zool 68:619–640
- Løkkeborg S, Ivar S, Anne OH, Ferter CUK (2014) Towards more efficient longline
814 fisheries: fish feeding behaviour, bait characteristics and development of
alternative baits. Reviews in Fish Biology and Fisheries 24(4) 985–1003
- 816 Lorenzen K (2000) Allometry of natural mortality as a basis for assessing optimal release
size in fish-stocking programmes. Can J Fish Aquat Sci 57:2374–2381
- 818 Matsumura S, Arlinghaus R, Dieckmann U (2011) Assessing evolutionary consequences
of size-selective recreational fishing on multiple life-history traits, with an
820 application to northern pike (*Esox lucius*). Evol Ecol 25:711–735
- Matsumura S, Arlinghaus R, Dieckmann U (2012) Standardizing selection strengths to
822 study selection in the wild: a critical comparison and suggestions for the future.
Bioscience 62:1039–1054
- 824 McNamara JM, Houston AI, Collins EJ (2001) Optimality models in behavioral biology.
Siam Rev 43:413–466
- 826 Mee JA, Otto SP, Pauly D (2017) Evolution of movement rate increases the effectiveness
of marine reserves for the conservation of pelagic fishes. Evol

- 828 Appl:doi:10.1111/eva.12460
- Mittelbach GG, Ballew NG, Kjelson MK (2014) Fish behavioral types and their ecological
830 consequences. *Can J Fish Aquat Sci* 71:927–944
- Mollet FM, Poos JJ, Dieckmann U, Rijnsdorp AD (2016) Evolutionary impact assessment
832 of the North Sea plaice fishery. *Can J Fish Aquat Sci* 73:1126–1137
- Monk, C. T., Arlinghaus, R. (2017). Encountering a bait is necessary but insufficient to
834 explain individual variability in vulnerability to angling in two freshwater
benthivorous fish in the wild. *PLoS ONE* 12(3): e0173989
- 836 Mousseau TA, Roff DA (1987) Natural selection and the heritability of fitness
components. *Heredity (Edinb)* 59:181–197
- 838 Myers RA, Hoenig JM (1997) Direct estimates of gear selectivity from multiple tagging
experiments. *Can J Fish Aquat Sci* 54:1–9
- 840 Nakayama S, Rapp T, Arlinghaus R (2017) Fast–slow life history is correlated with
individual differences in movements and prey selection in an aquatic predator in
842 the wild. *J Anim Ecol*:in press
- Peterson I, Wroblewski J (1984) Mortality Rate of Fishes in the Pelagic Ecosystem. *Can J*
844 *Fish Aquat Sci* 41:1117–1120
- Philipp DP, Claussen JE, Koppelman JB, Stein JA, Cooke SJ, Suski CD, Wahl DH, Sutter
846 DAH, Arlinghaus R (2015) Fisheries-induced evolution in largemouth bass: linking
vulnerability to angling, parental care, and fitness. *Am Fish Soc Symp* 82:223–234
- 848 Pitcher TJ (1995) The impact of pelagic fish behaviour on fisheries. *Sci Mar* 59:295–306
- Poos JJ, Brännström Å, Dieckmann U (2011) Harvest-induced maturation evolution

- 850 under different life-history trade-offs and harvesting regimes. *J Theor Biol*
279:102–112
- 852 Quince C, Abrams PA, Shuter BJ, Lester NP (2008) Biphasic growth in fish I: theoretical
foundations. *J Theor Biol* 254:197–206
- 854 Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O (2010)
Personality and the emergence of the pace-of-life syndrome concept at the
856 population level. *Philos Trans R Soc B Biol Sci* 365:4051–4063
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal
858 temperament within ecology and evolution. *Biol Rev* 82:291–318
- Roff DA (1983) An allocation model of growth and reproduction in fish. *Can J Fish Aquat*
860 *Sci* 40:1395–1404
- Sheldon RW, Sutcliffe Jr. WH, Paranjape MA (1977) Structure of pelagic food chain and
862 relationship between plankton and fish production. *J Fish Res Board Canada*
34:2344–2353
- 864 Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: An ecological and evolutionary
overview. *Trends Ecol Evol* 19:372–378
- 866 Stamps JA (2007) Growth-mortality tradeoffs and “personality traits” in animals. *Ecol*
Lett 10:355–363
- 868 Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Sutter DAH, Suski CD, Philipp DP, Klefoth T, Wahl DH, Kersten P, Cooke SJ, Arlinghaus R
870 (2012) Recreational fishing selectively captures individuals with the highest fitness
potential. *Proc Natl Acad Sci U S A* 109:20960–20965

- 872 Thériault V, Garant D, Bernatchez L, Dodson JJ (2007) Heritability of life-history tactics
and genetic correlation with body size in a natural population of brook charr
874 (*Salvelinus fontinalis*). *J Evol Biol* 20:2266–2277
- Tsuboi J, Morita K, Klefoth T, Endou S, Arlinghaus R, Moran P (2016) Behaviour-
876 mediated alteration of positively size-dependent vulnerability to angling in
response to historical fishing pressure in a freshwater salmonid. *Can J Fish Aquat*
878 *Sci* 73:461–468
- Uusi-Heikkilä S, Whiteley AR, Kuparinen A, Matsumura S, Venturelli PA, Wolter C, Slate
880 J, Primmer CR, Meinelt T, Killen SS, Bierbach D, Polverino G, Ludwig A, Arlinghaus R
(2015) The evolutionary legacy of size-selective harvesting extends from genes to
882 populations. *Evol Appl* 8:597–620
- Uusi-Heikkilä S, Wolter C, Klefoth T, Arlinghaus R (2008) A behavioral perspective on
884 fishing-induced evolution. *Trends Ecol Evol* 23:419–21
- Ware DM (1978) Bioenergetics of pelagic fish: theoretical change in swimming speed
886 and ration with body size. *J Fish Res Board Canada* 35:220–228
- Werner EE, Anholt BR (2014) Ecological consequences of the trade-off between growth
888 and mortality mediated by foraging activity. *Am Nat* 142:242–272
- West GB, Brown JH, Enquist BJ (2001) A general model for ontogenetic growth. *Nature*
890 413:628–631
- Wolf M, Doorn GS van, Leimar O, Weissing FJ (2007) Life-history trade-offs favour the
892 evolution of animal personalities. *Nature* 447:581–4
- Zimmermann F, Jørgensen C (2017) Taking animal breeding into the wild: regulation of

894 fishing gear can make fish stocks evolve higher productivity. Mar Ecol Prog Ser
563:185–195

896

898

900 Table 1. Value of parameters

Parameter	Value and units	Eq.
Reproductive investment	k_r (yr ⁻¹)	
Size at maturation	w_m (g)	
Boldness	τ	
Critical feeding level (1)	$f_c = 0.2$	4
Available food (2)	$R = 1$	2
Mortality constant (3)	$\alpha_p = 1.9$	9
Metabolic exponent (5)	$n = 3/4$	2
Max. consumption parameter	$A = 19 \text{ g}^{1-n}/\text{yr}$	2
(4)		
Activity coefficient (6)	$\epsilon_a = 0.8$	
Maturation rel. to W (7)	$\eta_m = 0.25$	
Heritability	$h^2 = 0.2$	15, 16
Coef. of variation of traits	$\sigma_x/\bar{x} = 0.2$	14

(1) Hartvig et al. (2011).

(2) Leads to a functional response where the individual neither starves nor is satiated. Corresponds to a resource concentration equal to the half-saturation coefficient.

(3) Gives a factor for the mortality $\alpha_p \hat{t} \approx 1.6 \text{ yr}^{-1} \text{ g}^{n-1}$, which

corresponds to the level of mortality used in Andersen and Beyer (2015).

(4) Set to correspond to the growth coefficient in Andersen and

Beyer (2015): $A \left(\frac{\hat{\tau}_R}{\hat{\tau}_{R+1}} - f_c \right) \approx 5 \text{ g}^{1-n}/\text{yr}$ at 10°C.

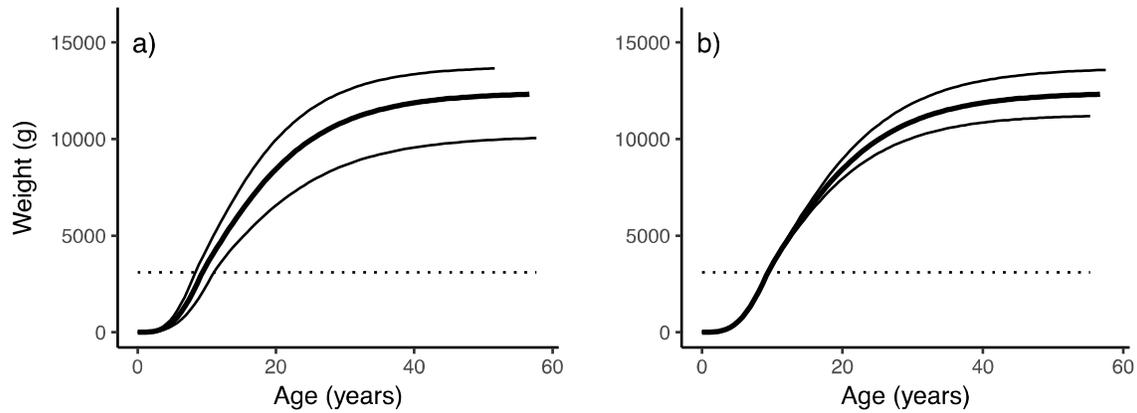
(5) West et al. (2001).

(6) Found by fitting observations of annual reproductive output

(Andersen and Beyer 2015)

(7) Beverton (1992).

902

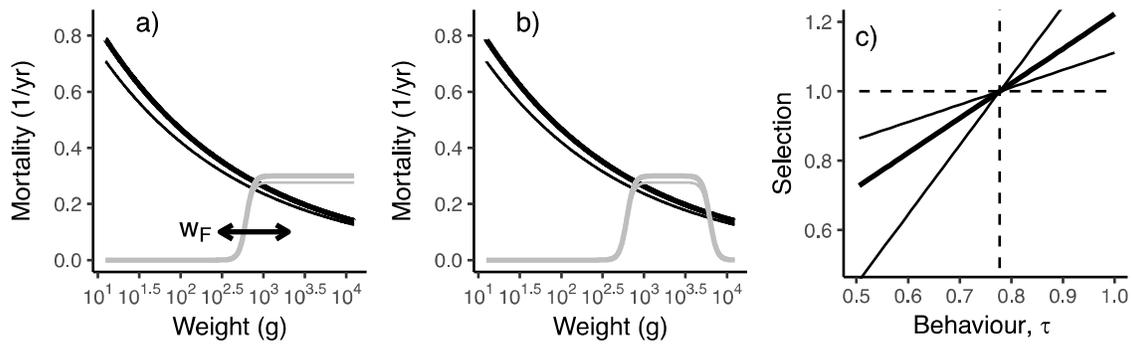


904

Figure 1. Size at age of a long-lived species with asymptotic weight of 14,000 g (thick
 906 lines). (a) Size at age with various boldness τ shown with thin lines for bolder individuals
 (above) and timid individuals (below). (b) Size at age with various investment in
 908 reproduction k_r ; higher investment (below) and less investment (above). The growth
 curves are drawn until 5 times the age at maturation.

910

912



914

Figure 2. Mortality and fisheries selectivity. (a+b) Predation mortality (black) and fishing

916

mortality (grey) for a species with asymptotic size 14,000 g with boldness $\tau = 0.9$

(thick) and $\tau = 0.8$ (thin) and fishing mortality $F_0 = 0.3 \text{ yr}^{-1}$. (a) Fisheries trawl selectivity

918

defined by the inflection point at w_F ; (b) harvest slot (aka gill-net) selectivity where the

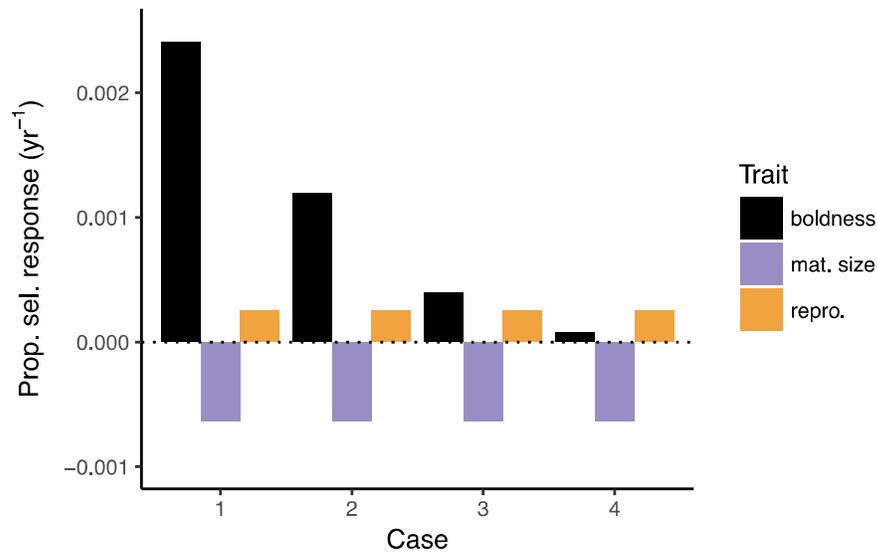
width is fixed and the entire slot is moved with w_F ; (c) Boldness-selective harvest for

920

three values of the selection strength b_F : 0 (horizontal dashed) and 0.5, 1 (thick line)

and 2.

922



924

Figure 3. Proportional selection response for four selectivity scenarios: 1: random

926

harvest; 2: size-selective harvest with a trawl-like selectivity; 3: boldness-selective

928

proportional selection response for: reproductive investment (orange), boldness τ

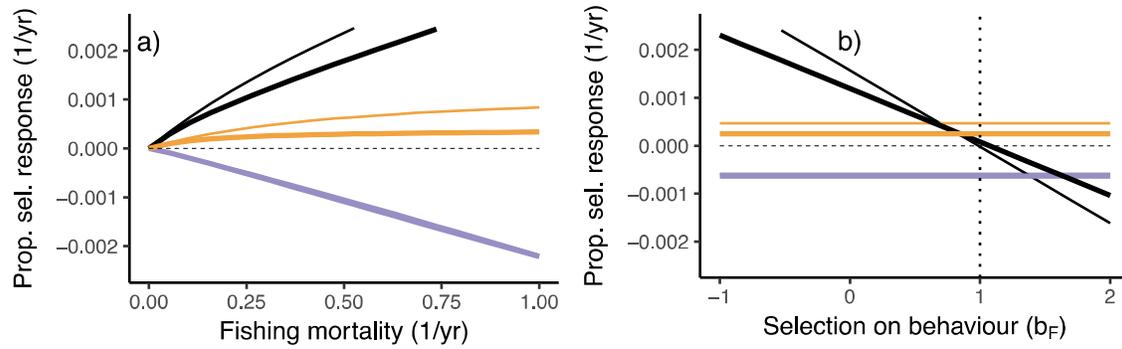
(black) and maturation size (magenta). Asymptotic size 14,000 g and fishing mortality

930

$F_0 = 0.3 \text{ yr}^{-1}$.

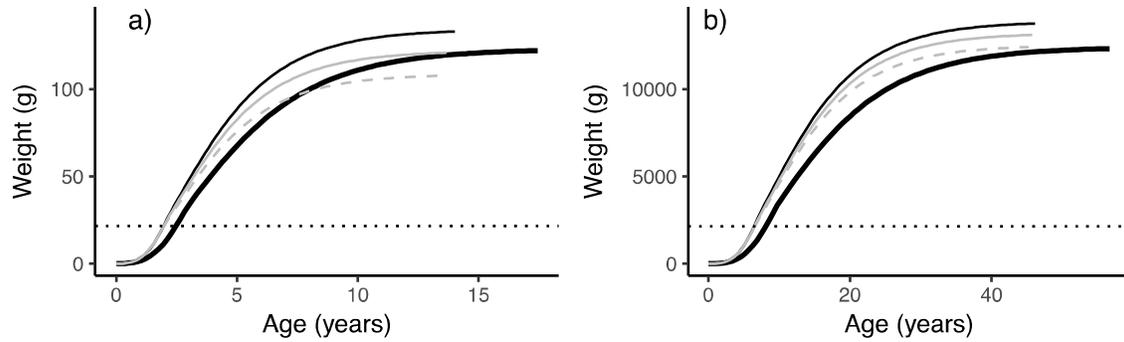
932

934



936 Figure 4. Proportional selection responses as a function of fishing mortality without
 938 selection on behavior ($b_F = 0$) (a) and as a function of the strength of selection on
 940 boldness for $F_0 = 0.3 \text{ yr}^{-1}$ for the case with a trawl-type size selection. Line width
 represents asymptotic size; thin: 140 g, thick: 14,000 g. The vertical dashed line in panel
 b corresponds to the selection on behavior used in Figure 3 for case 3. Reproductive
 investment (orange), boldness τ (black) and maturation size (magenta).

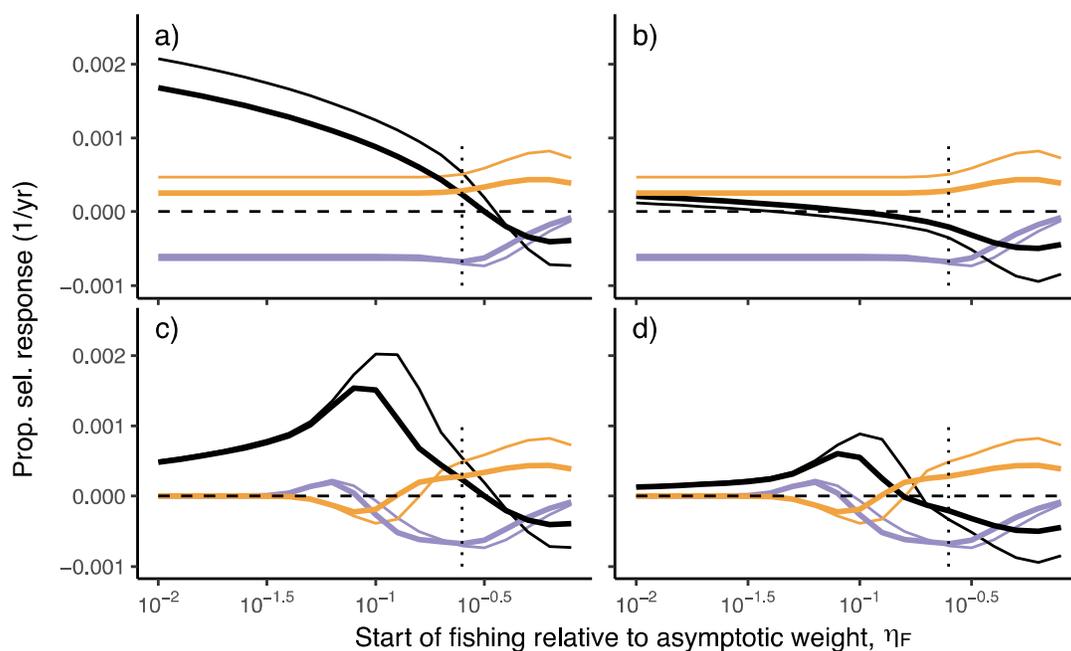
942



944 Figure 5. Size-at-age curves after 200 years of selection on species with asymptotic size
 140 g (a) and 14,000 g (b). Curves represent the three cases of selection: without
 946 selection (thick), after only size-dependent selection (case 2; thin), after selection on
 boldness only (irrespective of size) (case3; grey dashed), and combined selection on size
 948 and boldness (case 4; grey). The curves are drawn until 5 times the age at maturation to
 illustrate the effect of selection on age at maturation. $F_0 = 0.3 \text{ yr}^{-1}$; $b_F = 1$; the dotted
 950 line is at size at maturation.

952

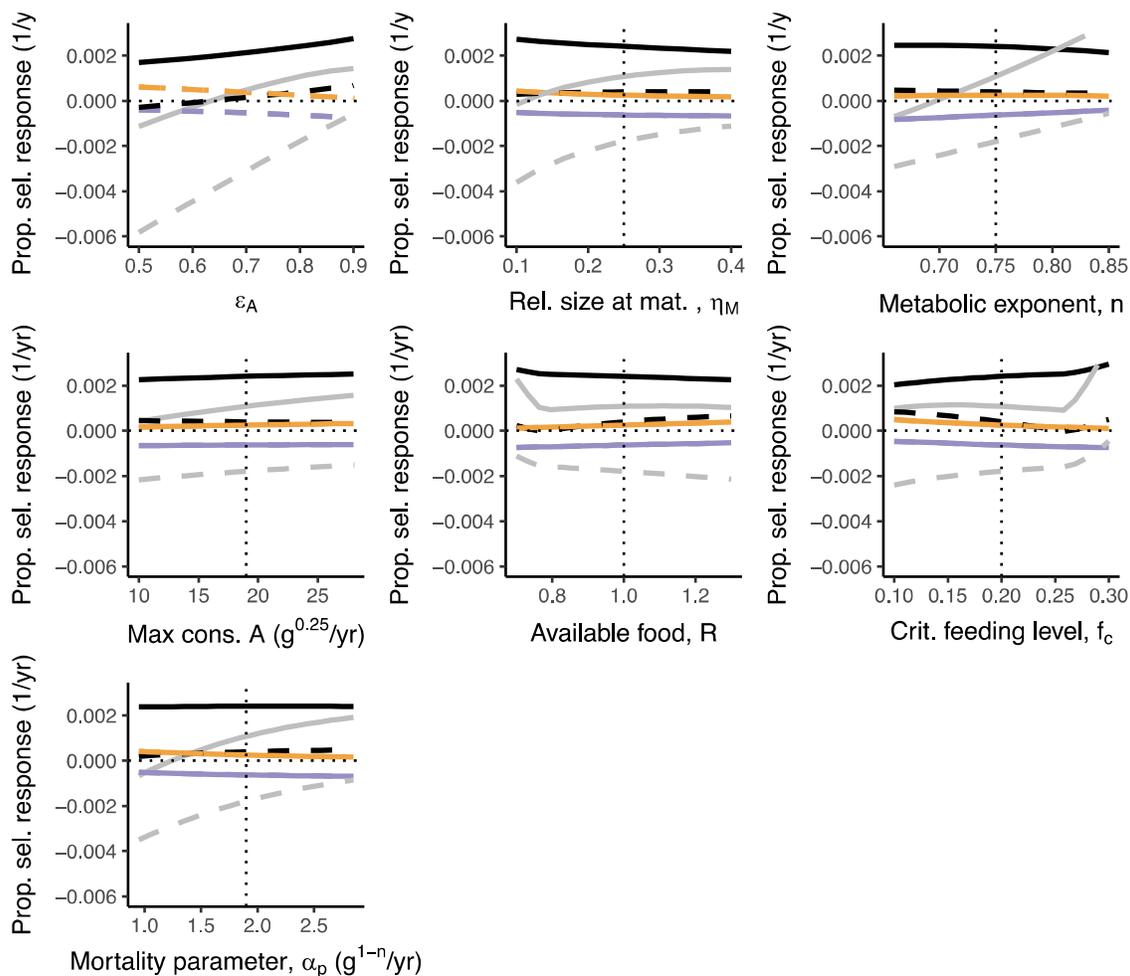
954



956

Figure 6. Proportional selection responses as functions of the mid-point of selectivity
 958 relative to asymptotic size (η_F) for a trawl selectivity pattern (Figure 2a) (a and b) and
 for a slotted size-selectivity (Figure 2b) (c and d). Panels a and c: without selection on
 960 boldness $b_F = 0$; panels b and d: with selection on boldness $b_F = 1$. Reproductive
 investment (orange), boldness τ (black) and maturation size (magenta). Vertical dotted
 962 line shows size at maturation. The case with entirely unselective mortality as baseline
 case corresponds to the left edge of panel a, while selection only on boldness
 964 corresponds to the left edge of panel b. Line width represents asymptotic size; thin: 140
 g, thick: 14,000 g.

966



968

970 Figure 7. Sensitivity of selection responses to changes in the fundamental parameters.

Reproductive investment (orange), boldness τ (black) and maturation size (magenta),

972 asymptotic size (grey). Solid lines are without selection on boldness $b_F = 0$; dashed

lines with selection on boldness $b_F = 1$.

974